

REVISION OF *PALMYRA SAVIGNY* (POLYCHAETA:APHRODITIDAE) AND REDESCRIPTION OF *PALMYRA AURIFERA*

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ABSTRACT

The polychaete genus *Palmyra* Savigny is revised; *P. aurifera* is redescribed and illustrated from museum and recently collected specimens from coral atolls and volcanic high islands of the Indo-Pacific. Relationships of the genus with members of the family Chrysopetalidae and Aphroditidae are discussed and reassessed based on characters examined in the present study. *Palmyra* is now placed in the family Aphroditidae, superfamily Aphroditacea.

KEYWORDS: Polychaeta, Aphroditidae, *Palmyra*, systematic relationships, Indo-Pacific.

INTRODUCTION

The genus *Palmyra* Savigny has had a confused taxonomic history. The genus has been variously included in the family Aphroditidae, Palmyridae and Chrysopetalidae. More recently, Day (1967) included the Chrysopetalidae in the Palmyridae. In view of the uncertainty, and as a part of my on-going study of the systematics of the family Chrysopetalidae (Watson Russell 1986, in press), clarification of the taxonomic status of the genus *Palmyra* is necessary. Relationship of the palmyrids to the family Aphroditidae has been suggested by a number of authors (c.g. Savigny in Lamarck 1818; Audouin and Milne Edwards 1832; Racovitza 1896; Grube 1878; Augener 1913, 1922; Pettibone in Perkins 1985). In this paper a comparison of the morphology of the palmyrids and aphroditids is used to assess the systematic position of *Palmyra* within the Aphroditidae.

Only 13 specimens of *Palmyra* exist in museum collections. All of these specimens were examined following the methodology developed during investigation of chrysopetalid setal patterns (Watson Russell 1986, in press). Due to their larger size and because few *Palmyra* specimens were available for study, setal types on every segment were examined *in situ* under a dissecting microscope and only some smaller anterior and posterior segments were excised and mounted on slides.

Material examined was borrowed from the following institutions: Allan Hancock Foundation, University of Southern California, Los Angeles (AHF); British Museum of Natural History, London (BMNH); Hamburg Zoological Museum (HZM); Muséum National Histoire Naturelle (MNHN); Northern Territory Museum, Darwin (NTM); National Museum of Natural History, Smithsonian Institution, Washington (USNM); Zoological Museum Berlin (ZMB); Zoological Museum Copenhagen (ZMC); Zoologisches Institut der Universität Wien, Vienna (ZUW).

HISTORICAL BACKGROUND

Lamarck (1818) first described the genus 'Palmyre' (= *Palmyra*) based on "Palmyre aurifere, Sav. Mss." (= *Palmyra aurifera* Savigny) and included it in 'Les Aphrodites'. Savigny's original manuscript description, dated 1809, was not published until 1820 (Hartman 1951:222). Savigny (1820:17, 1826:342) placed *Palmyra* as a genus within the tribe Aphrodites with a more detailed description than that given in Lamarck, and cited the original *Palmyra aurifera* as a "nouvelle et fort belle espèce" from the Isle de France, Mascarenes (= Mauritius). He also recorded another palmyrid specimen as "*N. palmifera* Cuv., Collect." from the Red Sea, as communicated to him by M. Cuvier. I have not been able to find any further reference to the specimen either in the literature or in the MNHN collections.

Blainville (1828:462) gave a brief description of *P. aurifera* and remarked on its similarity to that of the aphroditid group Hermiones. Audouin and Milne Edwards (1832:445, pl. 10, figs 1-6) included "le genre Palmyre de M. Savigny" within the tribe 'Aphrodisiens Nus' and referred to it as being distinguished from all other aphroditids by the absence of elytra and its similarity to members of the tribe Hermione. They also figured the species for the first time.

Grube (1850) briefly mentioned *Palmyra aurifera* and suggested it had similarities to the scaleworm *Eumolphe fragilis* Risso and the amphinomid *Spinther oniscoides* Johnson. Later, Grube (1855) described a small paleae-bearing polychaete from the Mediterranean as *Palmyra debilis* (= *Chrysopetalum debile*).

Kinberg (1858) created the Palmyracea as a family within the Aphroditea and defined it as lacking elytra; paleae on all segments; tubercles and dorsal cirri alternating. Schmarda (1861) placed *Palmyra* and his newly named genera *Paleanotus* and *Bhawania* in the family Palmyracea Kinberg. Claparède (1864) further described two small paleae-bearing forms from the Mediterranean: *Palmyra* (*Palmyrides*) *Portus Veneris* and *Palmyra* (*Palmyropsis*) *Evelinae*, as "deux Aphroditacés nouveaux du genre Palmyre". Examination of the descriptions of these species establishes that they belong to the Chrysopetalidae. Quatrefages (1865) included *Palmyra* and Schmarda's new genera in the family Palmyriens.

Ehlers (1864) erected a new family, Chrysopetalea (= Chrysopetalidae) to contain his new genus *Chrysopetalum*, *Paleanotus* Schmarda, *Bhawania* Schmarda, and questionably, *Palmyra* Savigny. In a paper entitled "Bemerkungen über die Familie der Aphroditen" Grube (1875) briefly discussed the problematic placement of *Palmyra*. He initially agreed with Audouin and Milne Edwards's separation of the aphroditids into the scaled and naked genera, the latter containing *Palmyra*. However, he suggested that Ehlers's family Chrysopetalacea, be united with Kinberg's family Palmyracea, and that the latter be excluded from the aphroditids. Grube (1878) later published a lengthy description of a specimen of *Palmyra aurifera* from Palau. He included *Palmyra* in the

Palmyracea and remarked on its similarity to the aphroditid genus *Pontogenia* Claparède.

In his study on the anterior end of *Chrysopetalum debile*, Racovitza (1896) came to the conclusion that it was impossible to unite *Chrysopetalum* and *Palmyra* (*sensu* Savigny) in the same family and remarked that *Palmyra* was perhaps a true cousin of the aphroditid genera *Pontogenia* and *Aphrogenia* Kinberg.

McIntosh (1885) identified a specimen collected by the *Challenger* from off Japan, as *Palmyra aurifera*?. He described it as possessing scales and compared it with the genus *Pontogenia*. Potts (1910) described two palmyrids from the Indian Ocean as *Palmyropsis macintoshi* and *Palmyra splendens*.

Augener (1913, 1922) offered a comprehensive review of *Palmyra aurifera* and made detailed reference to specimens of *Palmyra aurifera* collected from the Kingsmill Is (= Gilbert Is). In his 1913 paper, Augener designated McIntosh's *Challenger* specimen as 'non *Palmyra aurifera*' and considered it better placed in the aphroditid genus *Pontogenia* or *Aphrogenia*. In an extensive footnote Augener (1922:9-10) questioned the validity of Potts's species, and after noting the preoccupation of the name *Palmyropsis*, considered that both species should be referred to *P. aurifera*. My examination of McIntosh's and Potts's type-specimens in the BMNH confirms Augener's view. Augener pointed out that past confusion had led to an amalgamation of *Palmyra* with the smaller paleae-bearing chrysopetalid genera, and suggested that since *P. aurifera* obviously did not fit into the family Chrysopetalidae, then either the characters of the family Palmyridae should be emended or the monotypic genus *Palmyra* be incorporated into a new family for which he suggested the name Gymnaphroditidae, to be placed as a subfamily of the Aphroditidae. Horst (1917) maintained a similar view and suggested that *Palmyra* and *Palmyropsis* be included in Augener's proposed Gymnaphroditidae.

Subsequent workers did not adopt Augener's nomenclature. Chamberlin (1919) recognised the separate identities of the Chrysopetalidae and Palmyridae, and included *Palmyra* and *Palmyropsis* Potts in the latter family. Monro (1924) re-examined

McIntosh's *Challenger* specimen, placed it in the genus *Pontogenia* and, together with additional specimens collected from the China Sea, described it as a new species, *P. macintoshi*. Specimens in the BMNH, collected from New Britain, and represented only by a number of incomplete parapodia on slides, were labelled with unpublished names by Willey as '*Palmyra aurifera*, *Palmyra aurifera squamata* and *Palmyra japonica*'. As far as I can determine, all of these parapodia belong to the aphroditid genera *Pontogenia* and *Aphrogenia*.

Hartman (1954:631, fig. 174A) described four specimens from the Marshall Is. and figured the anterior end of *Palmyra aurifera*. In her Catalogue, Hartman (1959:125) cited the two families separately as Palmyridae and Chrysopetalidae. Day (1967:115) synonymised Chrysopetalidae with Palmyridae and the genus *Chrysopetalum* with *Paleanotus*.

Mileikovsky (1977) placed both families in the order Phyllocoemorpha. Fauchald (1977) listed the two families separately under the superfamily Chrysopetalacea within the suborder Aphroditiformia, order Phyllocoemida; Ushakov (1982) listed the two families in a similar manner to Fauchald, within the order Phyllocoemorpha. Pettibone (1982) made no reference to the palmyrids but cited the Chrysopetalidae as an aberrant family in the superfamily Aphroditacea. However, Perkins (1985) quotes Pettibone (in litt.) as including *Palmyra* in a subfamily of the Aphroditidae.

SYSTEMATICS

Superfamily Aphroditacea Johnson, 1839

Family Aphroditidae Malmgren, 1867

Description (after Pettibone 1966, 1982, in part - emended to include genus *Palmyra*). Body relatively large, broad, ovate or oblong; flattened ventrally, arched dorsally; less than 60 segments. Epidermis entirely or partly covered with small to large tubercles. Prostomium and segment 1 non-retractile or retractile within anterior segments (*Palmyra*). Prostomium subovate with sessile eyes or eyes on rounded or club-like ocular peduncles; single median antenna, comprising basal cerato-

phore and style; pair of long, smooth or ciliate ventral palps. Papillated facial tubercle ventral to median antenna, anterior to mouth, present or absent (*Heteraphrodita*). First or tentacular segment projecting anterolaterally and fused in part to prostomium, with 2 pairs of tentacular cirri and uniramous lobes with paleae and/or capillary setae. Following parapodia biramous, supported by 1 or 2 aciculae, with longer dorsal and shorter ventral cirri; cirri with clavate tips. Buccal or second segment with long ventral cirri lateral to mouth. Eversible pharynx elongate, muscular, with papillae around opening and non-chitinous plates; intestine with segmental caeca. *Aphrodita*, *Laetmonice*, *Pontogenia*, *Aphrogenia* and *Heteraphrodita* with 13-20 pairs of elytra located on segments 2, 4, 5 and 7, continuing alternately to segments 23 or 25, then on every third segment to posterior end; long dorsal cirri present on segments lacking elytra. Elytrophores large, transversely elongate, thin-walled. Dorsal tubercles, corresponding in position to elytrophores on cirriferous segments, transversely elongate, large, thin walled, with single or fimbriated papilla in medial-posterior position (*Aphrodita*, *Laetmonice*, *Pontogenia*, *Aphrogenia*, *Heteraphrodita*). *Palmyra* lacking elytra, elytrophores, dorsal tubercles or papilla; notopodia raised, elongate ridges with notosetal paleal fans on every segment; single paleal fans, numbering 13 pairs, on segments 2, 4, 5, 7-25; double paleal fans and dorsal cirri on segments 3, 6, 8, continuing on alternate segments to 26, thereafter on segments 27, 29, 30, 32, 33. Notosetae simple, of several kinds: main notosetal fan of stout, erect spines (*Aphrodita*), some with barbed or harpoon shaped tips (*Laetmonice*) or flattened paleal setae curving over the dorsum with or without serrated margins (*Palmyra*, *Pontogenia*, *Aphrogenia*), or main notosetal fan absent (*Heteraphrodita*); capillary setae extending dorsally forming feltage, covering elytra (*Aphrodita*, *Heteraphrodita*, some species of *Pontogenia* and *Laetmonice*); iridescent, laterally produced capillary setae (*Aphrodita*, *Heteraphrodita*) and/or short or long lateral capillary setae with varying degrees of development. Notosetal types alternate (*i.e.* presence/absence) in all genera except *Palmyra*. Neuropodia conical, with many tiered or relatively few stout, dark

simple neurosetae; numerous lower bipinnate neurosetae present on segments 2 and 3 (*Palmyra*, *Pontogenia*, *Aphrogenia*, *Laetmonice*, *Aphrodita*) or absent (*Heteraphrodita*); additional neurosetal types found in anterior and/or posterior segments of *Laetmonice* and *Aphrodita*. Pygidium very small and rarely visible in posterior segments.

Characters distinguishing palmyrids and chrysopetalids. The palmyrids and chrysopetalids are two distinct groups with major differences of the anterior end, setal types and their arrangement on the body, and overall body shape and size.

The prostomium of palmyrids is of the aphroditid type with a long biarticulate median antenna, eyes on club-like peduncles, two long, tapered palps and a large facial tubercle situated in an anteroventral position. The prostomium of chrysopetalids is composed of a short median antenna, two lateral antennae, two cylindrical or ovoid palps, sessile eyes and a dorsal nuchal organ. The form of the chrysopetalid prostomium has some similarities to those of syllid and hesionid polychaetes.

Palmyrids are large, broadly ovate worms with a tough tuberculate skin. Notosetae consist of stiff paleae in a rosette formation and small lateral fascicles of capillary setae; a small fascicle of simple neurosetae is present on all segments with additional bipinnate neurosetae on segments 2 and 3. Dorsal cirri and type of paleal fan alternate on mid-body segments. Chrysopetalids are small, elongate, and often very fragile. Setae consist of paleal and/or spinous notosetae (the former group inserted in a transverse row on the dorsum) and dense fascicles of compound neurosetae. There is no alternation of dorsal cirri and/or notosetal types; dorsal cirri and a similar type of paleal fan are found on all mid-body segments.

The one character that is immediately obvious and similar in both palmyrids and chrysopetalids is the possession of golden, notosetal paleal fans that imbricate down the dorsum. However, chrysopetalids possess paleal and spinous setae with an internally chambered box-like structure (Watson Russell, unpublished [paper given at the International Polychaete Conference, Sydney, 1983]; Perkins 1985). All other polychaete paleal types, including those belonging to

Palmyra have an uncompartmented, longitudinally arranged, tubular type of internal structure.

In view of the differences in morphology of palmyrids and chrysopetalids and the similarities of the palmyrids and aphroditids, the family Palmyridae can no longer be included within the superfamily Chrysopetalacea. The Chrysopetalidae is retained as the single family within the Chrysopetalacea. Chrysopetalids share certain morphological and structural characteristics with the hesionid, syllid and nereid families of the superorder Nereidiformia. The systematic position of the family Chrysopetalidae will be elucidated in future papers.

Relationships of *Palmyra* within the Aphroditidae. Possession of dorsal cirri on alternate body segments (*i.e.* 3, 6, 8 etc.) allies *Palmyra* with the scaleworm families of the superfamily Aphroditacea. Relationship between the palmyrids and aphroditids (family Aphroditidae Malmgren, 1867) is indicated by a comparison of characters. Characters shared between *Palmyra* and other aphroditid genera are: (1) overall body shape with a limited number of segments; tuberculate skin; (2) similarity in overall shape, number and displacement of appendages and structure of the prostomium and segments 1 and 2; (3) overall shape of the elongate, muscular pharynx with papillate lip, intestine and segmental caeca; (4) possession of fascicles of large paleal or spinous notosetae that may alternate; (5) bipinnate neurosetae in anterior segments; (6) formation of developing oocytes along segmental blood vessels and their culmination in clusters around the segmental caeca; large, mature ova. Characters 1, 3, and 6 are also seen in variable states in other scaleworm families. The structure of the anterior end and the possession of fascicles of large, stout, notosetae that may alternate are characters shared at the family level by palmyrids and aphroditids. The family Palmyridae can no longer be sustained and it is therefore proposed that *Palmyra* be included as a genus within the family Aphroditidae, superfamily Aphroditacea.

Within the Aphroditidae *Palmyra* is most closely related to *Pontogenia*. Characters shared by these genera include: possession of paleae among setae of segment 1; a pattern of double and single paleal fans on the same

alternate segments (observed in palmyrids and two species of *Pontogenia*); capillary notosetae on all segments; palmyrid serrate paleae types similar to those seen in some *Pontogenia* species; clear distal 'cap' of eirri of *Palmyra* adults seen in juveniles and some adults of *Pontogenia*; posterior-most neurosetal types of young palmyrids seen in juvenile pontogeniids. *Palmyra* shares with *Pontogenia* and *Aphrogenia* the same type and number of adult neurosetae.

Characters defining the palmyrids are: retractile prostomium; tuberculate epidermis over the entire body; large, flattened paleae fans composed of broad, rounded paleae; alternation of notosetal types does not include presence/absence of any notosetal type; absence of elytra, elytophores and dorsal tubercles.

Origin and function of elytra and their absence in *Palmyra*. *Palmyra* differs from other known aphroditids in lacking elytra, elytophores and dorsal tubercles. However, it is uncertain whether the absence of these characters are primitive or derived.

The Lower Cambrian fossil record includes forms with possible annelid affinities that possess imbricating mineralized scales (sclerites of halkieriids - Jell 1981; Bengtson and Conway Morris 1984). The Burgess Shale material of the Middle Cambrian includes forms with flattened, paleae-like scales and erect spines (sclerites of wiwaxiids - Bengtson and Conway Morris 1984) and polychaetes with large notosetal fascicles of imbricating paleae (Conway Morris 1979). Jell (1981) ascribed a possible respiratory function to halkeriid sclerites but Bengtson and Conway Morris (1984) disagreed, suggesting that sclerites had a primarily protective function; they further hypothesized that the mode of respiration involved lifting of the sclerites to expose the dorsal surface in a manner analogous to that described for aphroditaccan polychaetes. Storch (1968) discussed the primary defensive/protective function of the large erect and flattened setae of the notopodia of certain polychaete families, Aphroditidae, Chrysopetalidae and Amphinomidae, that exhibited complex but primitive musculature.

From the fossil evidence it may be that fascicles of large notosetae (paleae and/or spines) and scales are primitive characters

within the Polychaeta and in particular the Aphroditacea.

Reduction of the notosetal fascicle is seen in species of Aphroditidae that have alternating notosetal types, but complete loss of the large notosetal spines is exhibited only by *Heteraphrodita*. Reduction of the notopodium and elytra, and loss of notosetae also has taken place in certain commensal species of Polynoidae (R. Hanley personal communication).

The only other example of a sealworm species in which elytra are absent is the aberrant interstitial sigalionid, *Metaxypsamma uebelackerae* Wolf, where the adult form retains neotenous characters. Wolf (1986) suggested that the absence of notopodia and elytra in *Metaxypsamma* conferred a narrower body which allowed better exploitation of interstitial spaces.

In scaled aphroditid genera the elytra serve to ensure the circulation of water over the thin-skinned dorsum which is considered to be the true respiratory surface (Fordham 1925; Van Dam 1940; Mettam 1971). Van Dam's opinion that during respiratory movements the elytra are depressed by muscular contraction of the elytophores and elevated by coelomic pressure was supported by Mettam's study of the muscular anatomy of these structures. The elongate, thin-walled elytophore on the elytragerous segment and the similar, thin-walled dorsal tubercle (with a single or fimbriated papilla) on the eirrigerous segment each contain the dorsal lobes of the segmental caeca. In aphroditids the dorsal sac of the caeca are multilobed and this may create a greater surface area for internal respiration.

Species of *Aphrogenia* and *Laetmonice*, which inhabit hard substrates, possess low-set elytophores and dorsal tubercles (with fimbriated or simple papilla), variable capillary notosetal development, and felt that is poorly-developed or absent. Species of *Aphrodita* and *Pontogenia*, which burrow in soft sediments, possess larger, elevated elytophores and dorsal tubercles (with a large fimbriated papilla), and well-developed notosetal fascicles of capillary setae and feltage. The larger, more raised elytophores and dorsal tubercles allows a large volume of water to pass over the dorsum, while the large fascicles of capillary setae are effective filters.

On the other hand, juveniles of *Aphrodita australis* and *Pontogenia chrysocoma*, that have been collected from hard substrates in shallow water, lack elytra, elytophores, dorsal tubercles and notosetal felt. At this early stage the major notosetal types (spines or paleae) are relatively large compared to the size of the body, and entirely cover the dorsum (Watson Russell in prep). The difference in the degree of development of the dorsal tubercle and papilla, elytophore, and certain notosetal types between adults and juveniles of *Aphrodita australis* and *Pontogenia chrysocoma* may be linked to the particular respiratory requirements of their respective habitats.

Palmyrids are restricted to crevices in hard substrates in clear, well-oxygenated oceanic waters, and the absence of elytra may be linked to the respiratory regime of their habitat.

Little is known of the relationships of scale-worm families, and revision of other aphroditid genera is necessary before the phylogenetic position of *Palmyra* within the Aphroditidae can be elucidated.

Palmyra Savigny

Palmyra Savigny in Lamarck, 1818: 20 (type species *Palmyra aurifera* Savigny in Lamarck, 1818, by monotypy). Gender: feminine.

Palmyropsis Potts, 1910:326 (type species *Palmyropsis macintoshi* Potts, 1910, by monotypy).

Diagnosis. Body broad, rectangular; anterior and posterior segments slightly tapered. Maximum segment number less than 40. Thick epidermis with globular papillae covers body. Prostomium with median antenna; two pairs of eyes on raised peduncles; two long palps; large facial tubercle. Segment 1 fused to prostomium with 2 pairs tentacular cirri; short, erect paleae fascicle, 2 fascicles capillary notosetac. Prostomium, segment 1 retractile in anterior segments. Large, folded mouth opening posterior to palps; elongate muscular pharynx; intestine with paired segmental caeca. Large, flattened fascicles of broad paleae imbricate down and across dorsum covering it entirely or leaving partly bare medial strip; paleae of anteriormost and posteriormost segments with margins serrate,

faintly serrate on distal tips only or non-serrated entirely. Lateral small notopodial lobes with capillary setae; capillary fascicles thick, sparse or absent. Double paleal fans and dorsal cirri alternate (on segments 6-26) with single paleal fans (on segments 7-25); dorsal cirri double up on posteriormost segments. Lower bipinnate neurosetae on segments 2 and 3; simple bidentate neurosetae from segment 2. Pygidium not visible.

Description. *Prostomium:* *Palmyra* possesses a small prostomium with a short to medium length median antenna inserted on a broad, papillate ceratophore mid-dorsally on the prostomium. Each eye is composed of a coalesced pair of eyespots on an extended or retracted peduncle. Two long tapering palps with minute hairs and an elongate, marginally papillate facial tubercle are present (Fig. 2A,B). The median antenna, tentacular cirri, dorsal and ventral cirri are all composed of two articles in tandem; both articles are narrowed proximally and inflated distally with a half-rounded, clear, lens-like cap most distally (Fig. 1K).

Peristomium - Segment 1: Uniramous segment 1 supports a pair of tentacular cirri and a small anterior fascicle of erect paleal setae and posterior fascicles of short, relatively broad capillaries (Figs 1A, 3A). Segment 1, in conjunction with the prostomium, can be retracted within the anterior segments so that only the tips of the prostomial and peristomial cirri are visible; it is in this position that the eye peduncles appear retracted.

Segments 2-6: Segment 2 (buccal segment), 3 and subsequent segments are biramous. The notopodia of segment 2 are directed anteriorly and support a small, almost circular paleal fan and a fascicle of capillary setae. The neuropodia are small, with a fascicle of slender bidentate setae and a small lower, dense or sparse fascicle of golden bipinnate setae (Fig. 3C,D); ventral cirri or buccal cirri, the same length as the tentacular cirri, are situated on large cirrophores on each side of the mouth (Fig. 2B). Segment 3 has similar, slightly larger notopodia than segment 2 and dorsal cirri; neuropodia possess bidentate and bipinnate fascicles of neurosetae and short ventral cirri. Segments 4 and 5 have paleal and capillary notosetal fascicles and no dorsal cirri; neuropodia have 4 stout, brown bidentate setae and ventral cirri. Segment 6 has

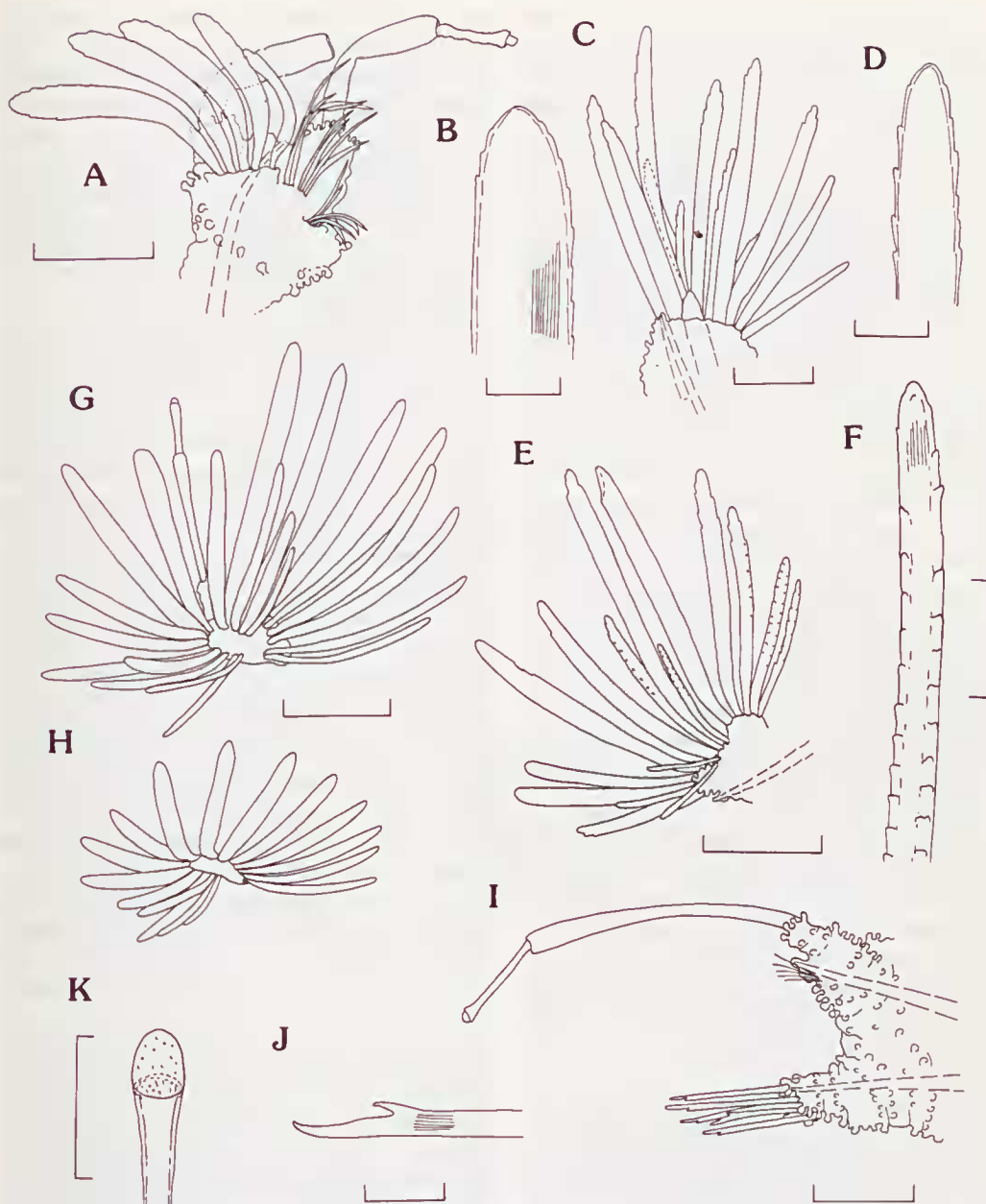


Fig. 1. *Palmyra aurifera* A-D, I-K, holotype MNHN UC92; E, F BMNH ZK 1224.3.1.149; G, H ZUW V.2180: A, parapodium from segment 1; B, detail of palea from same; C, notopodium from segment 29, anterior view; D, detail of palea from same; E, notopodium from segment 20, anterior view; F, detail of palea from same; G, double paleal fans of notopodium from segment 16, anterior view; H, single paleal fan of notopodium from segment 9, anterior view; I, parapodia from segment 29, anterior view, paleal notosetae not shown; J, detail of neuroseta from same; K, detail of distal end of dorsal cirrus from same. Acicula dashed A, C, E, I. Scales A, C, I = 0.4mm; B, D, F, J = 0.1mm; E, K = 0.2mm; G, H = 0.8mm.

notopodia with dorsal cirri and notosetae consisting of a lateral paleal fan with an overlapping medial fan; this arrangement is termed a 'double fan' (Figs 1G, 2H). Segment 7 has notopodia with no dorsal cirri and one

paleal fan, termed a 'single fan' (Figs 1H, 2I). Paleal fans insert in a full or half rosette pattern in the notopodia.

Notosetae: Palmyrid paleae of midbody segments are long, symmetrical with rounded

or pointed tips and smooth margins, pale golden to dark bronze-gold in colour. Several specimens have encrusting white, calcareous zooid organisms, resembling bryzoans, on the superior paleal surfaces; the same type of encrustation has also been observed on the ventral surface of worms. The notoaciculum is large and prominent within the notosetal fascicle. Double and single paleal fans are not well delineated in the anteriormost and posteriormost segments; the two posteriormost notopodia are very small with tiny setal fascicles. Paleal fans of the anteriormost and posteriormost segments have smaller numbers of paleae than those on the mid-body; single paleal fans have smaller numbers of paleae when compared with double paleal fans (Table 1, 2). The shortest paleac originate at lateral and medial points within the fan. All paleae have internal longitudinal striae and thickened margins. Capillary notosetae originate from a small, laterally positioned fascicle below the paleal fan and notoaciculum (Fig. 11); they are often short and blade-like in the anterior segments (Figs 1A, 3A), becoming long and thin, with minute hairs in mid body segments. Capillary setal development is highly variable (Table 1, 2).

Alternation of notosetal types: Alternation of certain notosetal types involving presence/absence occurs in all aphroditid genera except *Palmyra*. The major palmyrid notosetal type (*i.e.* paleac) is present on all segments but double fascicles of paleae occur on the cirriferous segments and single fascicles of paleae occur on the non-cirriferous segments. The lateral capillary fascicle is present on all notopodia.

Neurosetae: Palmyrids possess one type of simple neurosetae from segment 4 onwards. Neurosetae are stout, bidentate, golden brown in colour and number 4 (Fig. 3I,K); in an exceptional case one neuropodium had 5 (Fig. 11). A large dark brown neuroaciculum protrudes its distal tip into the neurosetal fascicle. Neurosetae of the posterior segments are paler in colour and more slender with elongate tips (Fig. 11,J). All neurosetae have internal longitudinal striae and thickened margins. An additional small fascicle of bipinnate neurosetae is present in segments 2 and 3 in all palmyrid specimens (Fig. 3C,D).

Pharynx, Intestine and Caeca: Dissection of the palmyrid ventrum reveals the pharynx, intestine and segmental caeca (Fig. 2C). The

pharynx is an elongate, maroon or pink coloured, muscular, flattened organ distally broad with a thick lip obscured by a membranous structure. Dissection of the pharynx reveals the lip overlaid with a dense fringe of elongate, purple coloured papillae; a number of thick muscular protrusions, not horny or chitinous in any way, are located on the inner side of the lip. The pharynx narrows proximally at the point of juncture with the thin walled intestine.

Segmental pairs of caeca arise at regular intervals from the dorsolateral sides of the intestine. In a 37 segment specimen (ZMC) 24 pairs were present, and a 30 segment specimen (AHF n.10159) possessed 18 pairs of caeca; in both worms the caeca started around segment 6 and ended about 6 segments from the posterior end. The anterior caeca are directed anteriorly on long necks (Fig. 2C); subsequent caeca have shorter necks and are directed laterally. The caeca of the former specimen were composed of a slender neck leading from the intestine to a large yellow coloured ventral sac. At the base of this sac, only visible in dorsal view, another short neck curved dorsally through a small space between intersecting muscle bands and, when teased out with forceps, is seen to end in a small dorsal sac that lies in the notopodial cavity (Fig. 2D). The 19th to 24th pairs of dorsal caecal sacs were bifurcated. The 30 segment specimen has large, blind ventral caecal sacs, coloured purple in part from its internal contents; there is no sign of the dorsal sac.

Epidermis: The thick, ridged epidermis of palmyrids varies in colour from grey to yellowish to an almost iridescent white. The segments are marked dorsally by raised, elongate notopodia which are joined by a narrow, raised ridge across the mid-body segments (Fig. 41). There are breaks along this ridge between the notopodia of the posterior segments (Fig. 4J). In the medial area between the notopodial ridges of two segments are additional raised ridges. Shallower papillate ridges traverse the ventrum and form a circular pattern around the parapodia. The skin between these raised ridges and laterally between the notopodia is much thinner. Raised globular papillae have a canal that connects sub-dermally (Fig. 3J); they are conspicuous on all raised ridges and scattered across the thinner skin. The extensive folding of the

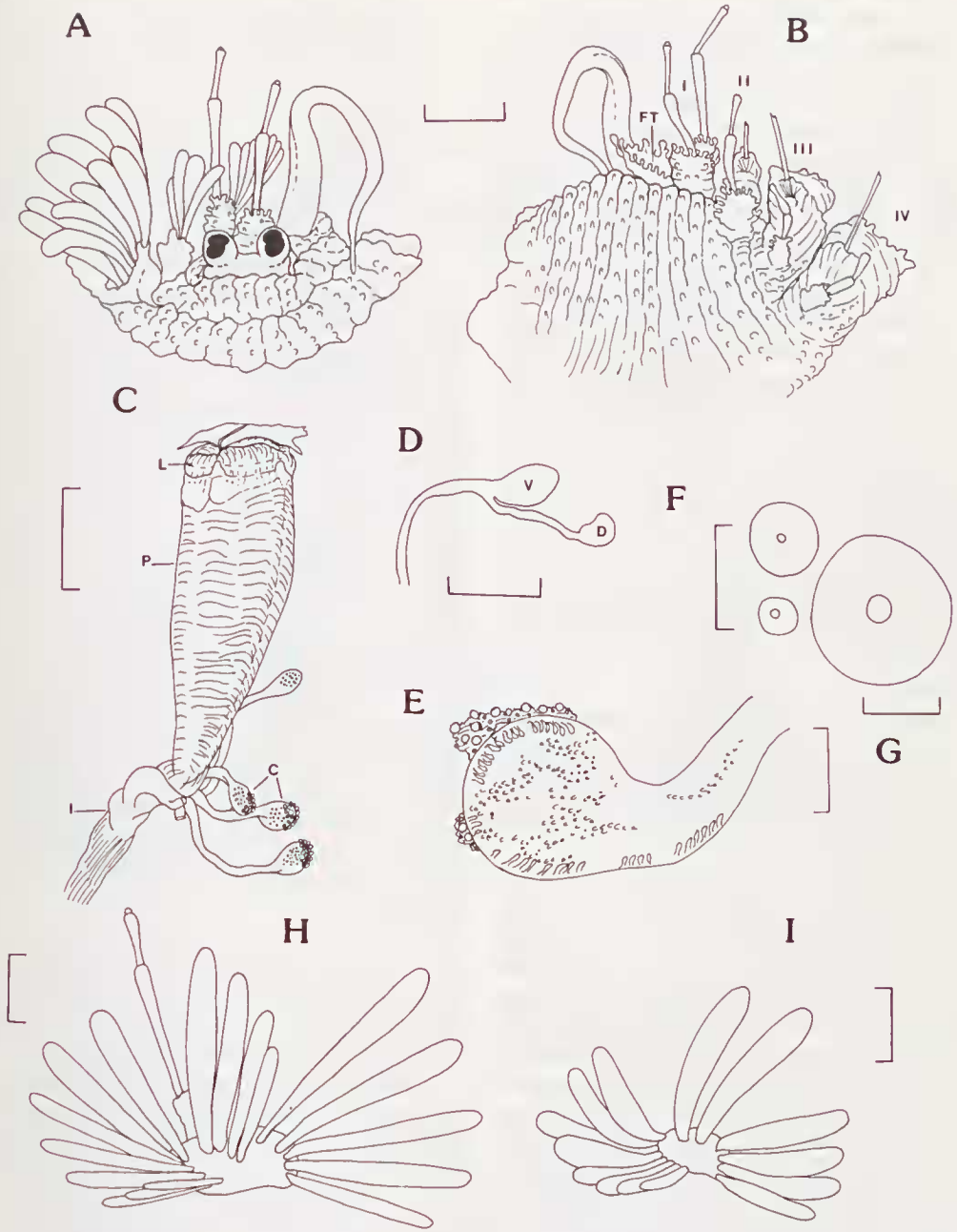


Fig. 2. *Palmyra aurifera* A,B USNM 29971; C, E-I, AHF n. I0159; D ZMC: A, anterior end, dorsal view, paleal fan of left notopodium 3 pinned back to reveal prostomium, left palp and anterior 3 right parapodia missing; B, same, ventral view, paleal fans not drawn. Abbreviations: FT, facial tubercle; I, parapodia I; II, parapodia 2.; III, parapodia 3; IV, parapodia 4; C, eacea; I, intestine; L, lip; P, pharynx; D, detail of caeca from segment 6, not in natural position, showing ventral sac (V) and dorsal sac (D); E, ventral sac with remains of egg cluster, detail of C; F, developing oocytes; G, mature egg from coelom; H, double paleal fans and dorsal cirrus of notopodium from segment 14; I, single paleal fan of notopodium from segment 5. Scales A,B = 0.4mm; C = 3mm; D = 1mm; E = 0.5mm; F = 0.1mm; G = 0.2mm; H,I = 0.6mm.

epidermis and the presence of papillae probably increases the respiratory surface area.

Biology. The reproductive biology of palmyrids is unknown. No palmyrid larvae or individuals under 28 segments have been reported. During dissection, I found large yolky eggs, 300-400µm in diameter (Fig. 2G), floating free in the coelom of *P. aurifera* (AHF n.10159). Developing oocytes of two sizes, 35µm and 60µm in diameter, were visible on the segmental blood vessels and terminated in clusters around the ventral caeca (Fig. 2E,F). In another specimen, developing oocytes measured 60µm and 170µm (HZM V.636). No nephridial papillae, such as those seen in other aphroditid genera have been observed in palmyrids although Grube (1878) reported "an opening on several rear parapodia on the abdominal side which probably correspond to the abdominal papillae of Polynoids". The large size of the mature eggs, at the top of the range for oocyte diameter observed in the Polychaeta (Olive 1985), suggests either an abbreviated non-feeding pelagic phase or direct development in *Palmyra*.

Remarks. *Palmyra* contains a single species (Tables 1 and 2 list and compare characters of 13 specimens). *Palmyra* is most closely related to *Pontogenia* within the Aphroditidae (see Relationships of *Palmyra* within the Aphroditidae).

A number of non-palmyrid species have been previously referred to the genus *Palmyra*: *Palmyra ocellata* Johnston 1827, has been synonymised with the sigalionid species *Pholoe minuta*; *Palmyra obscura* Müller 1858, was later included by Grube (1868) in his genus *Psectra* (based on Grube's description, specimens of *P. obscura* appear to belong to the chrysopetalid genus *Bhawania*); *Palmyra (Psectra)* sp.? of Ehlers (1887) from Florida is obviously a non-palmyrid as the given number of segments is 220; and *Palmyra? elongata* Grube 1856 from the West Indies belongs to the chrysopetalid genus *Chrysopetalum* (Perkins 1985).

Palmyra aurifera Savigny

(Plate IA,B, Figs 1A-K, 2A-I, 3A-K, 4A-J; Table 1, 2)

Palmyra aurifera Savigny in Lamarck, 1818: 305 [Ile de France, Indian Ocean]; Savigny 1820: 17; 1826: 341-342; Blainville 1828:

462-463; Audouin and Milne Edwards 1832: 445-446, Pl.10 Figs 1-6; Oken 1832: 942; Grube 1850: 286-287; 1875: 57-59; 1878: 12-15; Augener 1913: 80-83; 1922: 9-10; Chamberlin 1919: 92; Hartman 1954: 630, Fig. 174 A.

Palmyropsis macintoshi Potts, 1909: 370; 1910: 326, Pl.45 Fig. 18; Pl.46 Figs 21,22. *Palmyra splendens* Potts, 1910: 327, Pl.20 Fig. 25, Pl.21 Fig. 34.

Type material. HOLOTYPE - Indian Ocean, Mascarenes, 'Isle de France' = Mauritius, MNHN UC92, coll. M. Mathieu, 1818. [Note: I examined the holotype in the MNHN in September, 1986. The vial containing the specimen has two labels: one label has a red border (denoting type) and the printed annotation 'Palmyra aurifera Sav. Ile de France, M. Mathieu. A (R) - 1868 - NO.45a.'; the other label has hand written in ink 'M. Mathieu (individu décrit par Savigny 1836, 1838)'. Dr Renaud-Mornant, Laboratoire des Vers, considers that the erroneous dates on both labels are "no doubt a misprint..."].

Additional material. WESTERN INDIAN OCEAN. Mascarenes: Mauritius, taken out of a hole in sponge, 100 fthms (182m), 1, BMHN ZK 1924 3.1.149, (holotype of *Palmyropsis macintoshi*), coll. Percy Sladen Trust Expedition, Indian Ocean, 1905; Cargados Carajos, Stn B2, 30 fthms (55m), 1, BMHN ZK 1924.3.1.80 (syntype of *Palmyra splendens*), coll. same as previous; Réunion I., 1, ZUW V2180.

EASTERN INDIAN OCEAN. Western Timor Sea: N.W. Australia, Ashmore Reef, under a piece of coal among coral rubble in shallow pool, on reef flat at low tide, 1, NTM W.5054, coll. R. Hanley, 15 April 1987.

PACIFIC OCEAN. Central Pacific: Marshall Is, Ifaluk Atoll, north of Klungalap, reef flats and coral heads, 1m, 1, USNM 29971, coll. Bayr et al, 4th Pacific Atoll Survey Team, Station 775, 28 October 1953; Enewetak Atoll, Lidilbut I., crevices of coralline algae, 2, AHF n.10159; Kingsmill Is = Gilbert Is, 1, ZMC (no registration number available), coll. Putze (note on back of label 'specimen probably purchased by Steenstrup from Putze, a German from Berlin who dealt with natural history specimens. Information from Jorgen Knudsen, July 1982 - M.E. Petersen'); same locality and collector as previous, 1, ZMB 1282; Viti = Fiji, 1, HZM V637; Marquesas, Nukahiva = Nuku Hiva, 1, HZM

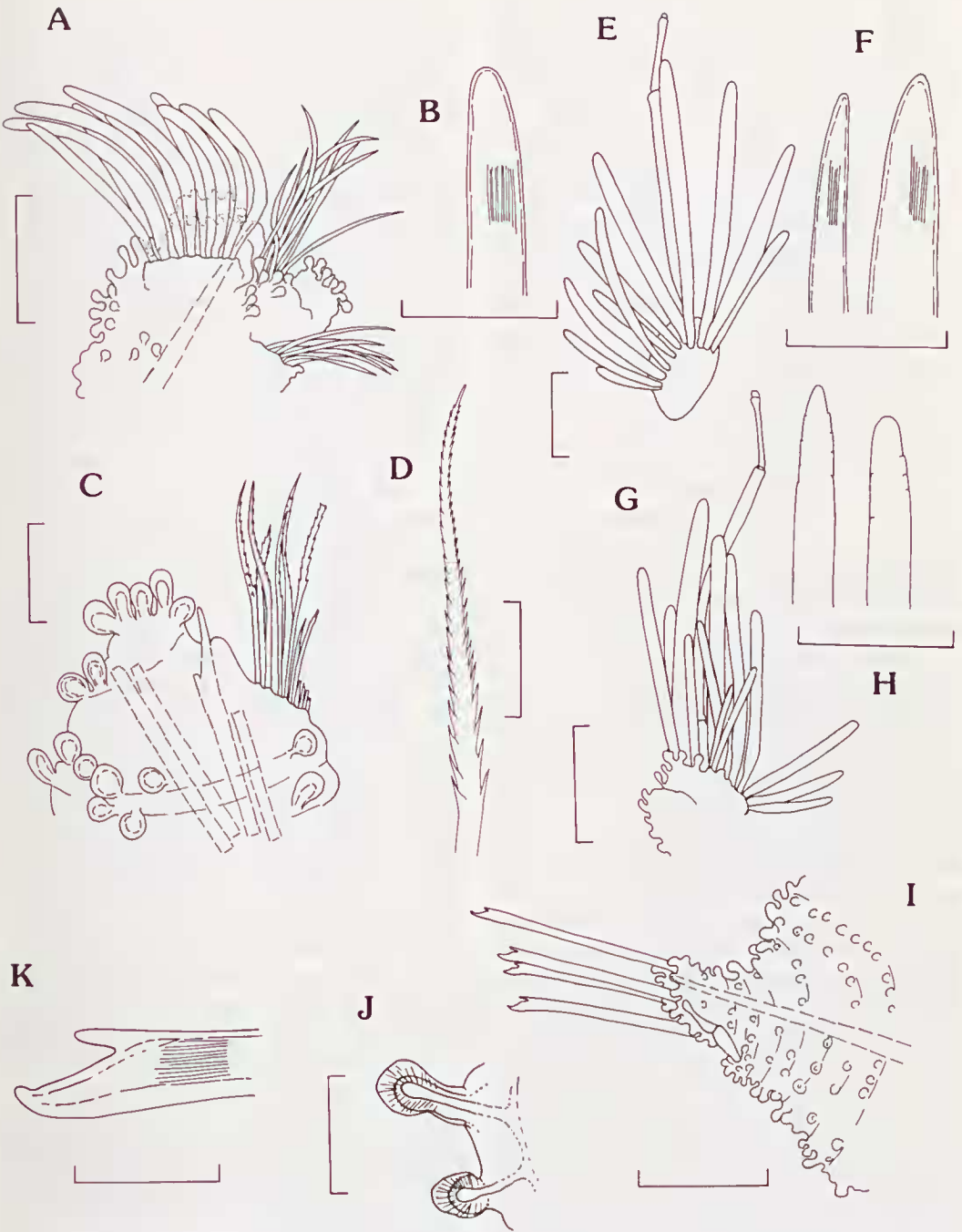


Fig. 3. *Palmyra aurifera* A,B ZMB 1282; C,D ZMC; E,F HZM V.636; G,H USNM 29971; I-K AHF n.10159: A, parapodium segment 1; B, detail of palea from same; C, neuropodium of segment 3, ventrolateral view, bidentate neurosetae dashed; D, detail of bipinnate neuroseta from same; E, notopodium of segment 36, anterior view; F, detail of paleae from same; G, notopodium of segment 34, anterior view; H, detail of paleae from same; I, neuropodium from mid-body, posterior view; J, detail of papillae from same; K, detail of neuroseta from same. Acicula dashed in A and I. Scales A,I = 0.4mm; B,C,F,H = 0.1mm; E = 0.2mm; G = 0.5mm; D,J = 0.04mm; K = 0.05mm.

V636; Coral Sea, Chesterfield Reefs, 19° 14' S, 158° 30' E, in crevice of coral rubble block covered with algae, 32-52m, dredged, I, NTM W.5138, coll. ORSTOM 1988 Chesterfield Reef Expedition, R. Hanley, 25 July 1988.

Description. Holotype entire, 30 segments, length 24mm, width 6mm. Broad, distally rounded paleae in fans, brassy golden in colour, imbricate dorsally; whitish encrustations present on ventrum. Long incision present on ventrum, pharynx entire inside. Prostomium and segment 1 partly retracted within segment 2. Median antenna on large ceratophore between two pairs of fused eyes on pedunculate ommatophores. Right palp entire, left palp damaged. Large convoluted facial tubercle clearly visible in ventral view, located between palps. Segment 1 small, reduced; notopodium uniramous with large aciculum; small erect fascicle of 5 paleae, 3 larger ones with serrate margins in part, 2 smaller ones with only distal tips serrate; 2 small groups of blade-shaped capillaries below paleae fascicle; long dorsal and ventral tentacular cirri (Fig. 1A,B). Segment 2 biramous; no dorsal cirri, ventral cirri with large cirrophores adjacent to mouth, styles broken; notopodium with small fascicles of paleae and capillaries; neuropodium with 2 types of neurosetae: 4 stout, golden-brown, bidentate, simple setae in superior position and lower, smaller fascicle of bipinnate setae; 2 acicula present in notopodia and succeeding segments. Segment 3 with notopodium possessing dorsal cirrus, fan of 13 paleae in 3 rows with shortest paleae proximally, and lower fascicle of capillaries; neuropodium with small ventral cirrus and 2 types of neurosetae as in segment 2. Segments 4 and 5 with paleal fans of 13 paleae each with 4 shortest in medial position; no dorsal cirri; neuropodium with ventral cirrus and 4 simple bidentate neurosetae as found in all succeeding segments. Neurosetae of segments 29 and 30 with slender, elongate tips (Fig. 1J) numbering atypically 5 on segment 29 (Fig. 1I), 4 on segment 30. Some paleae of posterior 2 segments with serrate margins in part (Fig. 1C,D). Dorsal cirri and double paleal fans alternate with single palcae fans on non-cirrigerous segments from segment 6-26. Pygidium not visible.

Comments on western Indian Ocean material. All specimens of *Palmyra aurifera*

from the Mascarenes possessed paleae with some degree of serrated margins on the anterior two segments and on the posterior ten segments (Fig. 1B,D,F); the greatest degree of serration occurred in the smaller lateral and medial paleae of the fascicle. Potts's (1910:Pl.20, Fig. 25) figure of the second segment of *Palmyra splendens* (= *aurifera*) shows some distally serrate paleae. My examination of the posterior 3 segments of this same specimen showed similarly serrated paleae. Examination of *Palmyropsis macintoshi* (= *Palmyra aurifera*) showed the anterior paleae with serrations and also paleae within the posterior 10 segments (segment 20, Fig. 1E,F). The Réunion specimen also showed serrate paleae from segments 25-29.

Characters used by Potts as a basis for creating the new palmyrid genus, *Palmyropsis*, included sessile eyes and the almost complete lack of capillary setae. The specimen from Cargados Carajos, is one of the smallest palmyrids yet found (28 segments); it has smaller, 'finer' paleae fans of a much paler golden colour than those of larger worms. The anterior end is very retracted in this specimen and the globular eyes, which can only be seen in top view, appear sessile; this may be due to sudden contraction. The lack of capillary setae on some segments on this specimen is a condition also seen in some Pacific Ocean specimens; capillary development is a variable character observed both within and between individuals (Table 1, 2). An additional specimen belonging to *Palmyropsis macintoshi* was briefly described by Potts from the Seychelles "from a crack in a coral mass" at a depth of 37 fathoms (67m), and possessed a small capillary tuft on each segment. This specimen could not be located in the BMNH collections during a visit in 1986.

Potts (1910:Pl.21, Fig. 34) was the first author to figure the small lower bipinnate neurosetae on segments 2 and 3. They have been observed in all palmyrid specimens that I have examined.

Comments on eastern Indian Ocean and Pacific Ocean material. The paleal fans on the anterior, mid and posterior segments of specimens from the eastern Indian and Pacific Oceans showed some variability in the degree of serration on their margins. The young adult specimen from the Chesterfield

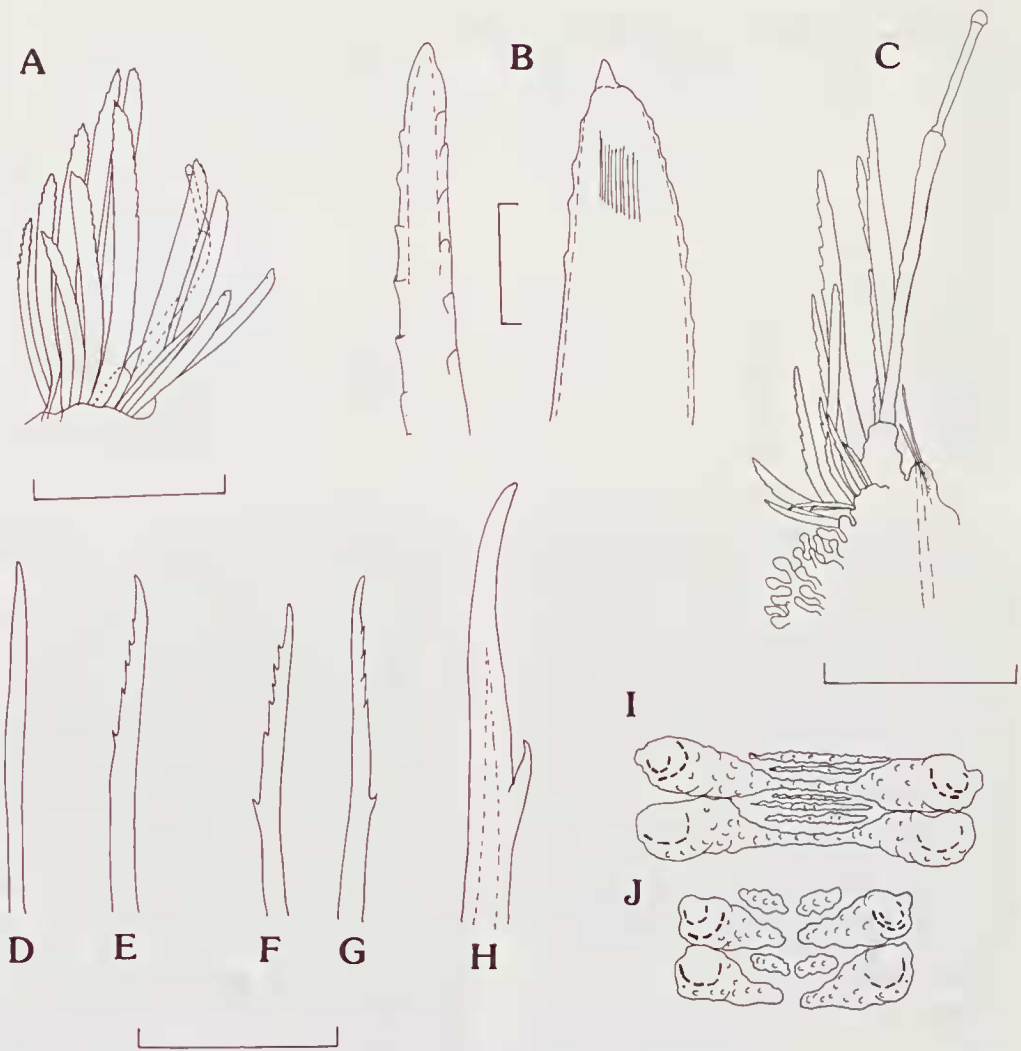


Fig. 4. *Palmyra aurifera* A-H NTM W.5138; I, J NTM W.5054: A, mid-body notopodium of segment 16, anterior view; B, detail of paleae from same; C, notopodium of segment 28, posterior view, aciculum dashed; D-H, neurosetal types from posterior 3 neuropodia; I, diagrammatic sketch of epidermal pattern on dorsum mid-body; J, same, posterior body, paleae insertion points dashed in I and J. Scales A, C = 1.00mm; B = 0.1mm; D-H = 0.04mm.

Reefs (NTM W.5138) possessed notosetal fans on all segments with nearly all paleae with some degree of serration on their margins (notopodium 16, Fig. 4A, B, C). Paleal fans of the posterior notopodia showed the greatest degree of margin serration on all paleae (notopodium 28, Fig. 4C). Paleae were long and slender; many with pointed tips (Fig. 4B).

Paleae with entirely smooth margins in notosetal fans on all body segments were found in adult specimens from Marquesas Is (HZM V. 636; notopodium 36, Fig. 3E, F),

Fiji, two specimens from the Marshall Is and one specimen from the Gilbert Is (ZMB 1282; parapodium 1, Fig. 3A, B). Another Gilbert Is specimen of 37 segments (ZMC) possessed small paleae on segments 1 and 2 bearing minute serrations on part of the margin. A similar condition was present in the anterior and posterior most segments of one specimen from the Marshall Is (USNM 29971; notopodium 34, Fig. 3G, H). On segment 2 of the Ashmore Reef specimen (NTM W.5054) there were faint serrations on the smallest, lateral palea. On segment 29 of this specimen

Table 1. Comparison of characters of *Palmyra aurifera* specimens (Indian Ocean).

Institution	MNHN	ZUW	BMNH	BMNH
Reg. No.	UC92	V.2180	ZK 1924.3.1.80	ZK 1924.3.1.149
No. segments	30	29	31	28
Length (mm)	24	15	25	12
Width (mm)	6	8	9	6
No. paleae:				
Anterior seg. single fan	13	16	—	—
Anterior seg. double fan	13	—	—	—
Mid seg. single fan	15	17	14	—
Mid seg. double fan	18	18-23	—	16
Mid body capillary setae	sparse	sparse	sparse	sparse to absent
Ornamentation of paleae on posterior segments	serrate	serrate	serrate	serrate
No. neurosetae - mid segs.	4	4	4	4
Dorsal cirrus on segment no.	3,6,8...24,26,27	3,6,8...24,26,27	3,6,8...24,26,27,29,30,31	3,6,8...24,26,27

the 2 outermost paleae had minutely serrated tips. On segment 30 the 2 smallest innermost paleae of a lateral fan of 5 were minutely serrated as was the innermost palea of the larger medial fan of 10 paleae (*i.e.* 3 tiny paleae had some margin serration compared with 12 smooth paleae in the same notosetal fascicle). Five specimens out of a total of 8 adult Pacific specimens, from a wide range of localities, possessed smooth, non-serrated paleae margins. While in three specimens a small degree of serration was retained in paleae fans of the anterior and posterior segments, the majority of Pacific adult palmyrids appeared to lose all traces of paleae serration with growth.

Neuropodia 27 and 28 of the young adult Chesterfield specimen (NTM W.5138) possessed a number of neurosetal types. A smooth small neuroseta (Fig. 4D) and distally serrate small neurosetae with and without a well formed spur (Fig. 4E,F,G) were two types not observed before in palmyrid specimens. Slender bidentate neurosetae (Fig. 4H) are typical of those seen in posterior segments of adult specimens (*cf.* Fig. 1J).

The prostomium and segment 1 are retracted in the Chesterfield specimen and the eyes retracted to the same degree as that observed in the Cargados Carajos specimen. One specimen in particular had a relaxed anterior end (USNM 29971); the prostomium and anterior 3 segments were visible (right 3 parapodia missing; Fig. 2A) as was the facial tubercle in ventral view between the long palps (left palp missing; Fig. 2B). The median

antenna and tentacular cirri of this specimen are longer than those figured by Hartman (1954:631, Fig. 174a) for another specimen from the same locality. Differences in relative length of cirri was noted on a number of specimens, perhaps due to regeneration.

Size correlated to number of segments varies between specimens, and paleal colouration and capillary notosetal development are variable among Pacific island specimens (Table 2). The large Marquesas worm (HZM 636) (L 32mm, W 12mm and 37 segments), when compared with the Ashmore specimen (NTM 5054) (L 15mm, W 6mm and 30 segments), is more than twice as big. The former specimen has dark gold, stiff, robust, broad paleae; paleal fans do not interlock mid-dorsum, leaving it bare; capillary fascicles are small, stiff and sparse; and the epidermis is creamy coloured, very thick and conspicuously tuberculate. Paleae of the latter specimen are more slender and a pale gold colour with paleal fans just interlocking at the mid-dorsal line; capillary fascicles are feathery, bushy and comparatively longer; and the skin is pearly white and appears thinly opaque. Some of these differences (*e.g.* size, degree of robustness) may be due to age and/or sex but some characters, such as the degree of development of the capillary fascicle, is seen to be very variable both between and within individuals. The specimen from Fiji (HZM 637) has long, very well-developed capillary setae, numbering 30-40 on each segment. The two specimens from Enewetak Atoll (AHF 10159) are distinguished by a complete lack

Table 2. Comparison of characters of *Palmyra aurifera* specimens (Pacific Ocean).

Institution Reg. No.	NTM W.5054	HZM V.637	HZM V.636	ZMC	ZMB 1282	AIfF n.10159	AHF n.10159	USNM 29971	NTM W.5138
No. segments	30	30	37	37	39	30	31	35	28
Length (mm)	15	15	32	20	31	25	27	25	10.5
Width (mm)	6	8	12	7	12	9	12	6	5
No. Paleae:									
Anterior seg. single fan	14-16	—	12	12	--	14	14	13	10
Anterior seg. double fan	14-16	14	12	12-15	--	14	15	14	12
Mid seg. single fan	18	18	13-16	13	14	14	13-14	14	12
Mid seg. double fan	20	20	14-17	15-17	--	--	17	16	13-15
Mid body capillary setae	mod. well dev.	well dev.	sparse	sparse to mod.	sparse to mod.	absent	absent	very sparse	sparse to absent
Ornamentation of paleae on posterior segments	minutely serrate	non serrate	non serrate	minutely serrate	non serrate	non serrate	non serrate	minutely serrate	serrate
No. neurosetae -									
mid segs.	4	4	4	4	4	4	4	4	4
Dorsal cirrus on segment no.	3,6,8...24, 26,27,29	3,6,8...24, 26,27,29	3,6,8...24, 26,27,29,30,27,29,30,32, 32,33,35,36 33	3,6,8...24,26, 29,30,32,33	3...24,26,27, 29,30,32,33, 35,36,37	3,6,8... 24,26,27	3,6,8... 24,26,27	3,6,8...24,26,27, 29,30,32,33	3,6,8...24, 26,27,28,

of capillary setae on any segment, although the small notosetal lobe is evident. The variability of this character between individuals of *P. aurifera* from the Indian and Pacific Oceans may be due to setal loss at a certain developmental stage and later regeneration, or loss perhaps due to environmental factors.

Grube's (1878) specimen of 37 segments, reported from Palau in the West Caroline Is, is not in the ZMB or HZM collections and appears to be lost. His description was general and included no figures. His observation of a brown pigmented patch on each segment next to the median line was not seen in the comparatively fresh Chesterfield or Ashmore specimens.

Remarks. Twelve of the palmyrid specimens fall into two geographically separate groups, distinguished by the degree of paleal serration on the anterior and posterior segments: in western Indian Ocean specimens distinct serrations are present on the paleae, but these are absent or only very weakly developed in the paleae of Pacific Ocean specimens. In view of the probable limited dispersal of palmyrid larvae and the very conservative morphology of the adults, I initially thought that two species might be present. However, a thirteenth palmyrid specimen, recently collected from the Chesterfield Reefs in the south-western Pacific by Russell Hanley, led me to question this conclusion. Unlike all other material, this specimen

(NTM W.5138) has serrated paleae throughout the body. The Chesterfield specimen also is the smallest in size of all the palmyrids I examined, and has a number of characters that suggest it is a young adult. Sexually mature gametes were absent, and it possessed small numbers of paleae of the single and double notosetal fans. Certain setal types, not seen in more mature specimens, included slender, serrate, distally pointed paleae in most notosetal fans along the body, and smooth and serrate neurosetal types in the posteriormost segments.

Although paleal serration is much more developed in adults from the western Indian Ocean compared with adults from the Pacific Ocean, a correlation between body size and degree of paleal serration is not apparent between adults from the same region.

Until larger numbers of larval, juvenile and adult palmyrids from both regions can be collected and compared, I retain the species name *aurifera* for all specimens of *Palmyra*.

Distribution and Habitat. In the western Indian Ocean, *P. aurifera* is known only from the Mascarene Plateau, an area that consists of a series of submerged islands and shallow banks within the 1000 fathom line (Gardiner 1936), and includes the islands of Réunion, Mauritius, Caragados Carajos, and Seychelles. Réunion is a high volcanic island lacking coral reefs; Mauritius is volcanic, with

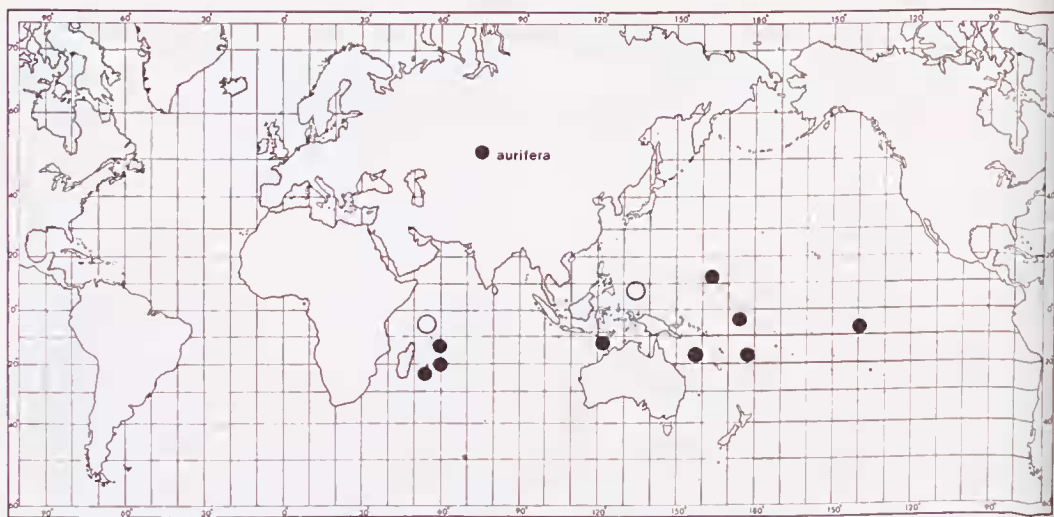


Fig. 5. Distribution map of *Palmyra aurifera*. Blank circle represents literature record only.

fringing coral reefs; Caragados Carajos consists of low-lying coral islands and sandy islets; and the Seychelles are of granitic origin, with fringing coral reefs.

In the eastern Indian Ocean, *Palmyra aurifera* has been collected from Ashmore Reef, off N.W. Australia. Ashmore Reef is a coral platform reef near the 200m line at the edge of the Sahul Shelf, an area close to the deep waters of the Timor Trough and the Wharton Deeps (Fairbridge 1950).

In the northern Pacific, *P. aurifera* occurs at Palau, Marshall Is, and Gilbert Is. The Palau group includes volcanic islands, coral atolls and submarine banks; the Marshall Is and Gilbert Is include coral atolls, islands, and raised and submerged banks.

In the south-western Pacific, *P. aurifera* has been collected at the Chesterfield Reefs and Fiji. The Chesterfield Reefs consist of coral atolls, and Fiji includes coral atolls and islands.

In the central Pacific *P. aurifera* occurs in the Marquesas, islands that are volcanic and lack coral formations.

Palmyra aurifera is largely restricted in its habitat to cracks and crevices in sponges, calcareous algae, and corals. In the western Indian Ocean, *P. aurifera* is known from depths down to 200m, but in the Pacific Ocean it occurs mainly in shallower waters to depths of 52m. In both the Indian and Pacific Oceans a common factor in the distribution of *P.*

aurifera is the presence of well-oxygenated, clean, and sediment-free water.

ZOOGEOGRAPHY OF PALMYRA

The widespread but isolated pattern of distribution of *Palmyra aurifera* (Fig. 5) and its restricted habitat, suggest that *P. aurifera* may be a remnant species with a previous distribution that may have been much broader and included continental margins. Evidence in support of this is the occurrence of *P. aurifera* at Ashmore Reef, a platform reef at the edge of the Australian continental shelf, and the Seychelles, an old rafted continental fragment.

It is interesting to speculate that the present day distribution of *Palmyra* is the result of the breakup of Gondwanaland. I hypothesise that an ancestral aphroditid fauna was originally present along the shelf of Gondwanaland, and that part of the fauna was rafted northwards by the Indian plate, and north-eastwards by the Australian plate after the breakup of Gondwanaland in the late Jurassic (Seyfert and Sirkin 1973). At 75 myr the Seychelles, Saya de Malha Banks, and the Chagos-Laccadive group were adjacent to the west coast of India. Rupture of the Seychelles, Saya de Malha Banks, and the the Chagos group from India occurred during its drift northwards at a latitude of about 30°S during the early Paleocene (Davies 1968). The volcanic parts of the

Chagos-Laccadive Ridge and the Mascarene Plateau were formed in the Eocene-Miocene, with the location of the volcanos controlled by a transform fault. This enormous transform fault, was responsible for the separation of the Chagos archipelago from the Mascarene Plateau during the formation of the Central Indian Ridge at 35 myr (McKenzie and Selater 1971). Dispersal of palmyrids in the western Indian Ocean probably occurred southwards from the Seychelles to Réunion, along the shallow banks and volcanic islands of the Mascarene Plateau.

Palmyrids have very large yolky eggs which suggests a probable non-feeding pelagic phase or direct development and only a very limited ability to disperse. The present pattern of distribution of *P. aurifera* is consistent with the limited dispersal ability of an old remnant species.

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